

# Oxygen Uptake and the Effect of Feeding in *Nautilus*

by

M. J. WELLS

Department of Zoology, University of Cambridge, Cambridge, U.K. CB2 3EJ,  
Lizard Island Research Station, Queensland, Australia

*Abstract.* Specimens of *Nautilus pompilius* (Linnaeus, 1758) and *N. stenomphalus* (Sowerby, 1849) were caught off the Great Barrier Reef. The animals can regulate their oxygen uptake successfully down to ambient  $PO_2$ s of 60 mm Hg and beyond at 10–20°C; some individuals reduced the  $PO_2$  in their respirometer to 15 mm Hg and lower before ventilation ceased; spontaneous recovery occurred when a well-oxygenated circulation was restored. The effect of feeding was investigated. There was no sign of a transient rise and fall in oxygen uptake following a meal, but some indication that, in the longer term, regular feeding or starvation could double or halve the metabolic rate. Oxygen uptake is very dependent on temperature, which would make the nightly vertical migrations into shallower, warmer water of considerable importance in terms of the animal's energy budget. A crude estimate of this budget suggests that a 500-g (flesh weight) *Nautilus* could maintain its normal activity pattern in the sea on about 2 g (wet weight) of fish per day; a good cropful would last it a month, or considerably longer, as metabolic rate falls in starvation.

## INTRODUCTION

*Nautilus* is the sole living representative of the many shelled cephalopod mollusks found in the fossil record. Morphologically, the shells of the four surviving species (*N. belauensis* Saunders, 1981; *N. macromphalus* Sowerby, 1849; *N. pompilius* Linnaeus, 1758; *N. scrobiculatus* Lightfoot, 1786; SAUNDERS, 1981) differ rather little from those of their Palaeozoic ancestors. There is every reason for studying the physiology and behavior of the modern animal; it is the only model for the extinct species that we have, and it is arguably more likely to resemble them in its habits and ecology than are the coleoids.

In 1985, *Nautilus pompilius* was trapped off the Great Barrier Reef near Lizard Island, Queensland, as part of a research program examining the distribution of *Nautilus* species (see SAUNDERS, 1981). As well as *N. pompilius*, specimens of *N. stenomphalus*, which may or may not be a valid species, were found. This was the first time that *N. stenomphalus* had been seen alive. As well as the known *N. stenomphalus* shell characteristics (open umbilicus and reduced shell pigmentation compared with *N. pompilius*, which it otherwise closely resembles), the animal has a distinct papillose hood. The data obtained gave no grounds for separating these two, but the availability of freshly caught *Nautilus* at a laboratory with some refrigeration facilities made possible the collection of fresh data on the capacity to regulate  $O_2$  uptake and to survive acute hy-

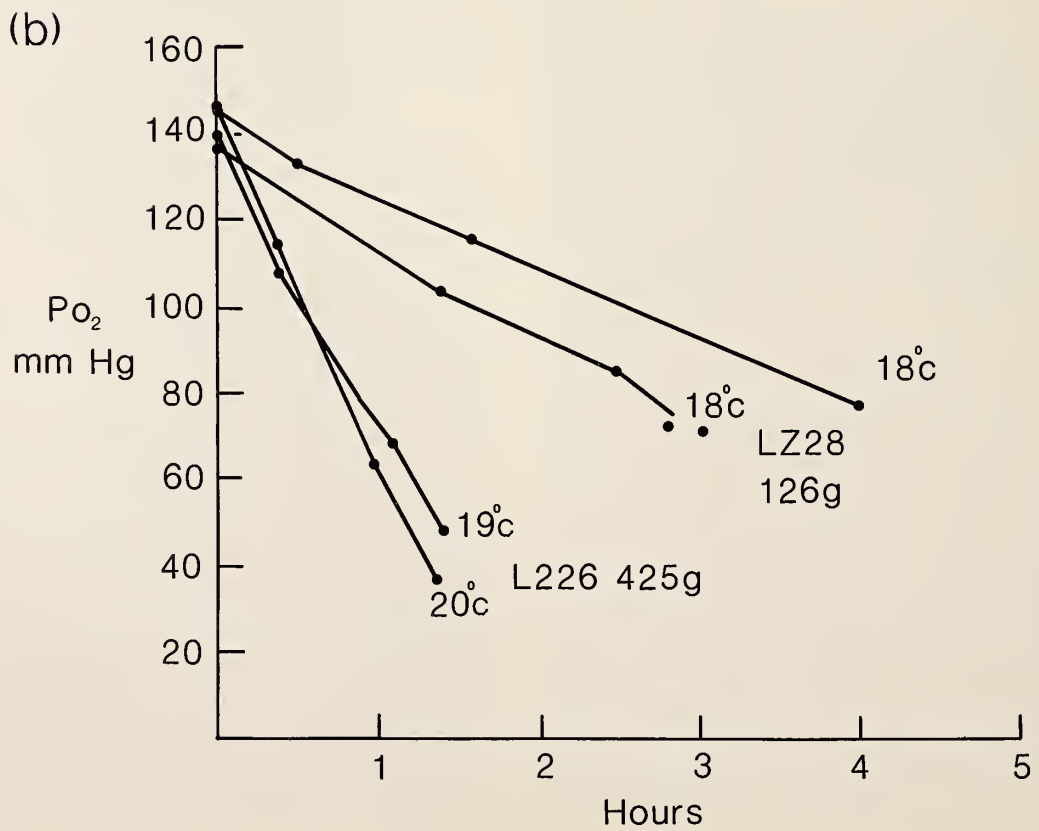
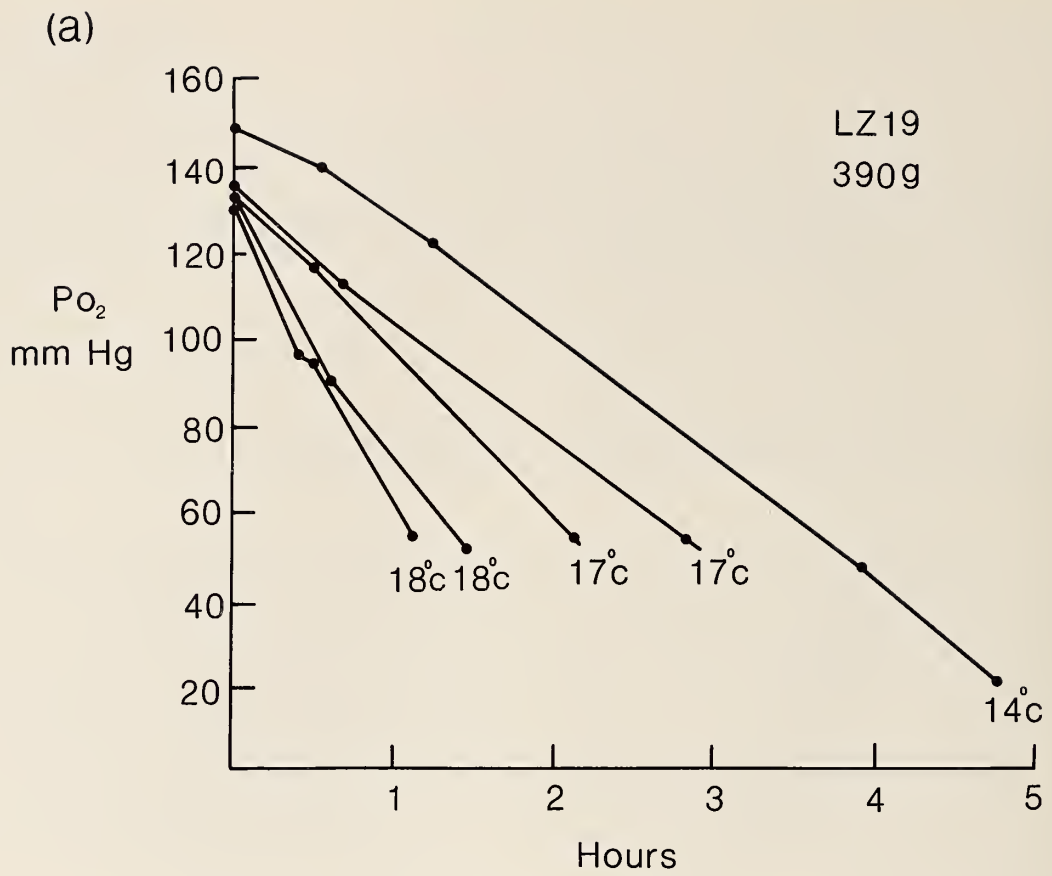
poxia, as well as information on metabolic rate and feeding, which is presented here.

## MATERIALS AND METHODS

*Nautilus* specimens were collected off Carter reef, 22 km (14 miles) NE of Lizard Island. Traps baited with dead fish and crabs were set on the fore-reef slope in 200 to 400 m from RVS *Sunbird* of the Lizard Island Research Station.

Animals for experiments were brought back to the laboratory in a refrigerated holding tank aboard RVS *Sunbird*. At the research station they were housed in a 220-L stock tank, aerated, and refrigerated; the flow of water through the stock tank (~250 mL/min) was used to adjust the temperature. Two 11-L respirometers were enclosed, and a refrigeration compartment built from polystyrene sheets around these and the holding tank, from which the respirometers were filled as required. Each respirometer had a floating lid of polystyrene, so that samples of the water could be run off through a compartment containing the electrode from an EIL 7130 oxygen analyzer and returned to the respirometer. Samples flowing past the oxygen probe were stirred magnetically. The electrode and collecting vessel (a beaker with a floating polystyrene lid) were enclosed in the same refrigerated space as the three aquaria.

Specific oxygen uptake figures are given in terms of flesh weight, measured when the animals were killed at the end



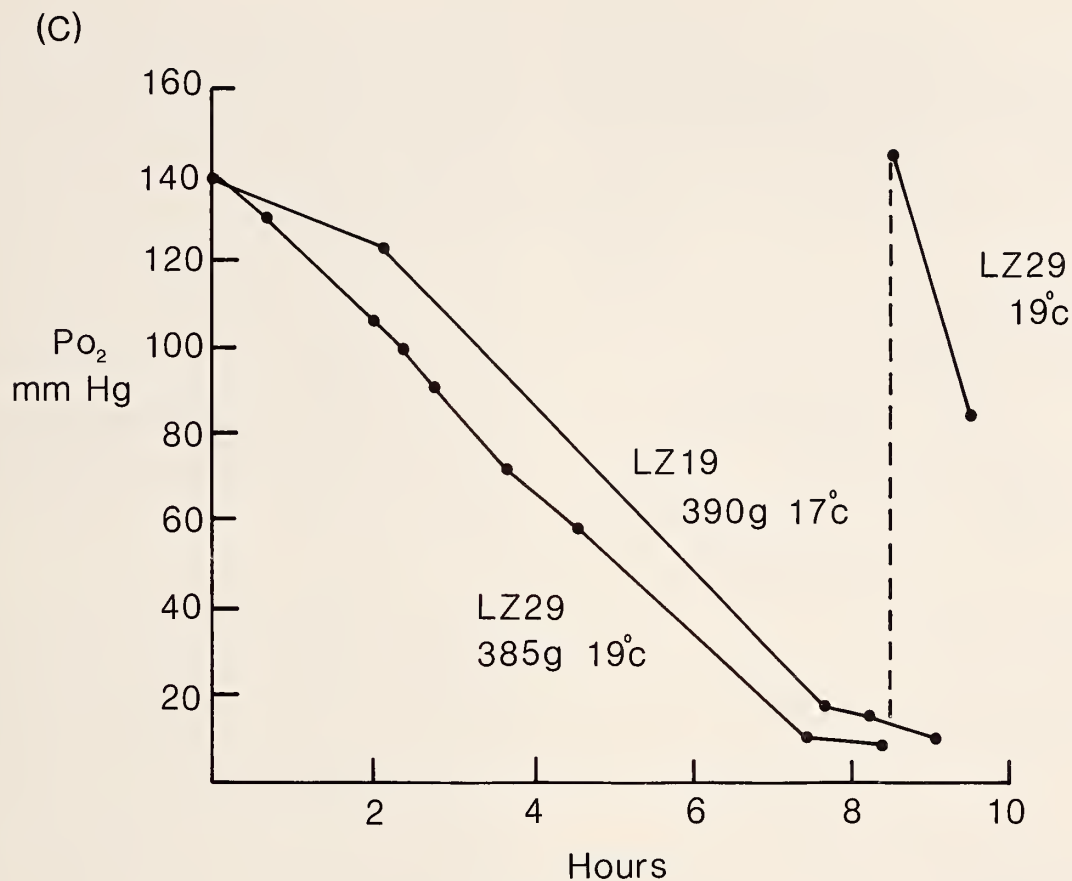


Figure 1

Regulation of oxygen uptake by *Nautilus* in closed respirometers. (a) five runs by a *N. pompilius*, LZ19 565 g, body wt. 390 g. (b) two runs by a juvenile *N. pompilius/stenomphalus* "hybrid," LZ28, 200 g, body wt. 126 g. And two by *N. pompilius*, LZ26, 655 g, body wt. 425 g. (c) two runs to very low oxygen levels by LZ19 and LZ29, another *N. pompilius/stenomphalus* "hybrid," 630 g, body wt. 385 g; in this plot, oxygen uptake is shown for a period immediately following transfer to well-aerated seawater. "Hybrids" are specimens showing a mixture of the characteristics of the two supposed species.

of the experiments. The oxygen content of the seawater at 100% saturation was taken from data given in CARPENTER (1966), assuming a chlorinity of 19.05, appropriate for Lizard Island in December.

The six animals used all remained in good condition throughout the period in the laboratory. Results from a seventh, which refused to feed at once when food was offered, were discarded.

## RESULTS

### Regulation of Oxygen Uptake

Because of the limitations imposed by refrigeration capacity, through-flow respirometry was impossible and oxygen uptake had to be measured from the reduction in PO<sub>2</sub> in a respirometer. It was therefore important to establish whether *Nautilus* can maintain its oxygen uptake in a declining ambient PO<sub>2</sub>. Reports on its capacity to regulate

in this manner have differed. REDMOND *et al.* (1978) showed that it could not do so at 25°C, whereas WELLS & WELLS (1985) found that the animals regulated successfully down at least to a PO<sub>2</sub> of 75 mm Hg in water at 17°C. Figure 1 summarizes a number of experiments made in which *Nautilus* progressively reduced the oxygen in their tanks down to PO<sub>2</sub>s of 60 mm Hg and beyond (exceptionally to less than 20 mm Hg) without apparently changing their rates of uptake, at least until levels of 30 mm Hg and below were reached. Thus, there is no doubt that this animal can regulate over a wide range at the temperatures it normally meets in the sea.

### Activity and Q<sub>10</sub>

Oxygen uptake rises by a factor of two or three times when *Nautilus* is jetting rather than sitting quietly at 18–20°C.

Table 1

*Nautilus*. Activity, animal size, and oxygen uptake in mL·kg<sup>-1</sup>·min<sup>-1</sup>, along with temperature during run and number of days since last feeding; representative values from runs lasting for 1 h or more and ending with PO<sub>2</sub>s above 60 mm Hg.

		No. days since last feeding
LZ19. <i>N. pompilius</i> . Mature male (565 g, body wt. 390 g).		
Active, while feeding	1.006 (19°C)	
Quiet	0.532 (19°C)	0
Quiet	0.207 (12°C)	4
LZ24. <i>N. stenomphalus</i> . Mature female (480 g, body wt. 310 g).		
Feeding	1.151 (21°C)	
Quiet	0.390 (18.5°C)	4
Quiet	0.189 (13°C)	5
LZ26. <i>N. pompilius</i> . Mature male (655 g, body wt. 425 g).		
Active	1.072 (20°C)	1
Quiet, following activity	0.814 (19°C)	1
LZ28. <i>N. pompilius/stenomphalus</i> "hybrid." Immature male (200 g, body wt. 126 g).		
Active	1.516 (18°C)	2
Quiet	0.499 (17.5°C)	4
LZ29. <i>N. pompilius/stenomphalus</i> "hybrid." Mature male (630 g, body wt. 385 g).		
After extreme hypoxia (see Figure 1c)	0.852 (19°C)	
Quiet	0.268 (17.5°C)	6
LZ30. <i>N. pompilius/stenomphalus</i> "hybrid." Mature male (810 g, body wt. 607 g).		
Active	0.605 (18°C)	4
Quiet	0.256 (17°C)	3

"Hybrids" were individuals showing a mixture of the characteristics of the two supposed species.

Figure 2 shows specific oxygen consumption plotted against temperatures for all runs lasting longer than 30 min made with mature animals at rest (or at least not noted as "active"; they were not kept under continuous observation). Oxygen uptake rises with increasing temperature, a matter that could be important to an animal that makes daily vertical migrations on reef slopes (WARD *et al.*, 1984). The Q<sub>10</sub> computable from this data is 4.3, but the scatter is large and little reliance should be placed on the accuracy of this figure.

Numbers alongside the outlying values in Figure 2 show the number of days since the individual concerned was last fed. Feeding increases the metabolic rate, fasting reduces it.

### The Capacity to Survive Periods of Acute Hypoxia

*Nautilus* can withdraw into its shell, blocking the entrance with the hood. As it cannot then ventilate, one would expect the animal to be resistant to intermittent hypoxia. In the present series of experiments animals were allowed to deplete the oxygen in their respirometers down to PO<sub>2</sub>s of 20 mm Hg and lower, on six occasions. In the two most extreme cases, ventilation eventually ceased. The tentacles of these animals were extended, flaccid, and the animals were, to all external appearances, dead. They nevertheless reacted at once when touched, drawing back into the shell and (or) beginning to ventilate afresh. Vigorous ventilation began when the seawater in the respirometer was aerated. In the single instance when oxygen uptake was measured immediately after the restoration of oxygen-rich seawater (see Figure 1), this was greatly enhanced, suggesting repayment of an oxygen debt. No attempt was made to quantify this.

### Effects of Feeding on Oxygen Uptake

Figure 3 summarizes the effect of feeding one animal five times in the course of nine days, four of the meals being on successive days. On three of the five occasions there was a marked rise in oxygen uptake just after feeding. This, however, appeared to be due to activity stimulated by feeding rather than feeding per se. Reasons for believing this are (1) the absence of a rise on the two days when the animal was *not* active after feeding and (2) the very short-term nature of the rise; it was over within an hour or two of feeding. It should be noted, too, that the peak at 10 days after capture occurred shortly *before* the animal was fed rather than after. In the longer term there is some indication that the average resting metabolic rate is elevated by repeated feedings. During the period of daily feedings on days 7–10 the resting rate rose to 0.6 mL·kg<sup>-1</sup>·min<sup>-1</sup> and then declined to 0.3 mL·kg<sup>-1</sup>·min<sup>-1</sup> in the three days fasting after this. Figure 2 shows the same effect; animals tested 2–6 days after feeding take up oxygen at only one-half to one-third of the rate of those tested within 24 h of a meal.

### DISCUSSION

Some of the results summarized above confirm statements already made elsewhere. Thus, it is now quite certain, despite some earlier doubts on the matter, that *Nautilus* can regulate its oxygen uptake over a wide range of ambient oxygen tensions.

The results following feeding were new and unexpected. By analogy with *Octopus vulgaris*, another opportunistic feeder, one might reasonably have expected a marked transient increase in oxygen uptake to follow the ingestion of a meal. No such surge was seen. Very little is known about digestion in *Nautilus* and nothing is published. The absence of large salivary glands (which produce quantities of proteolytic enzymes in coleoids), the small caecum, and the

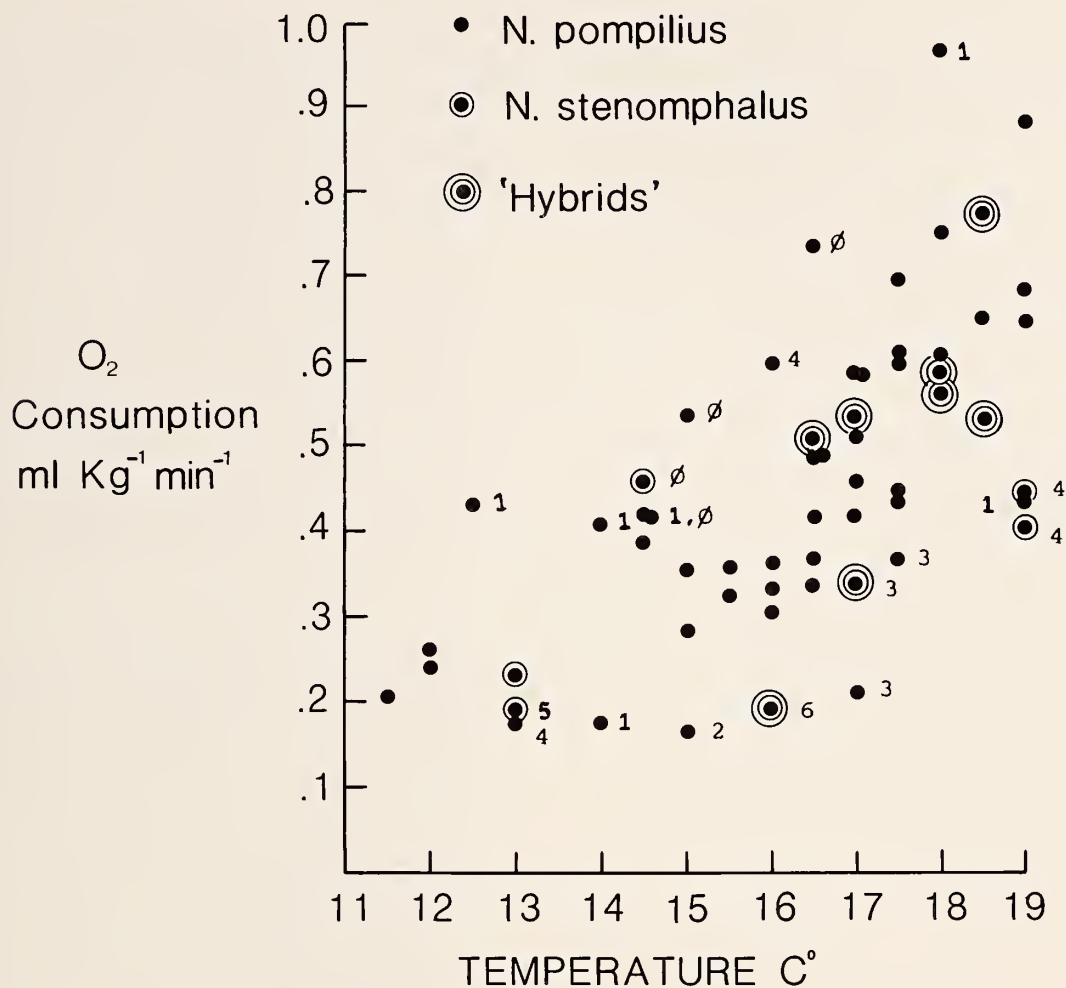


Figure 2

Oxygen uptake and temperature in *Nautilus*. Metabolic rate increased rapidly with temperature. Figures against outlying values show days since last fed.

unusual structure of the digestive gland (MANGOLD *et al.*, in press) all suggest that digestion is rather different from the system in coleoids (for review, see BOUCAUD-CAMON & BOUCHER-RODONI, 1983). Two facts from the present series of observations confirm the impression from the oxygen uptake experiments, that digestion in *Nautilus* is probably rather slow. One is the amount that animals would eat. All the individuals tested fed readily if presented with dead fish or pieces of crab, but they never took more than about 25 g of flesh. ZANN (1984) reported crop weights averaging more than 50 g from smaller animals caught in traps off Fiji. The implication is that the Lizard Island animals, first tested within a few days of arrival, were still "topping up" crops only part emptied after the last meal, having gorged themselves to repletion in the traps. The slow emptying of the crop was confirmed when animal LZ19 was killed. This *Nautilus* had not been fed for 3

days (see Figure 3) but it still had crab remains in the crop.

If digestion is as leisurely as these results suggest, it is likely that the great majority of the oxygen consumption figures that we have so far collected for *Nautilus* (REDMOND *et al.*, 1978; WELLS & WELLS, 1985, and in this account) are typical of fed rather than fasted animals, because all are derived from animals tested within a few days of capture in traps, where presumably, they gorged themselves. By analogy with *Octopus*, one would expect the metabolic rate to fall considerably in starvation. In view of the slow growth rate of *Nautilus* compared with other cephalopods (WARD, 1983) and the possible scarcity of catchable food in the depths where *Nautilus* lives, the possibility that the animal can cut its standard metabolic rate to low levels in lean times is important to our understanding of its ecology. The present series shows (Figures 2, 3) that oxygen uptake

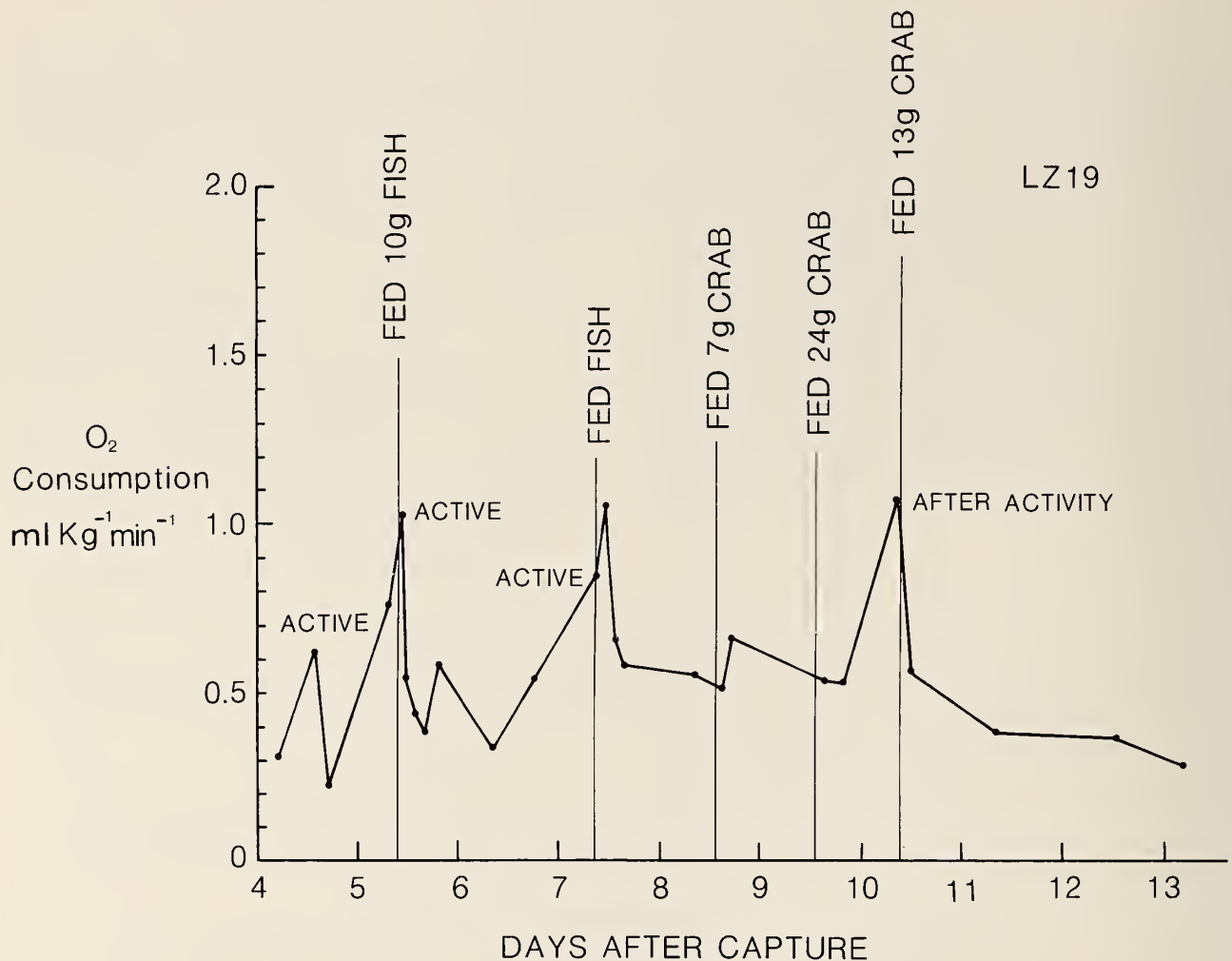


Figure 3

Metabolic rate and feeding history of *Nautilus pompilius* LZ19, body weight 390 g. "Active" means seen to be jettling about its respirometer at one or more spot checks made during oxygen uptake runs. The animal still had crab remains in the crop when killed 13 days after capture and 3 days after the last meal.

is reduced to one-half or even less by three days of fasting. We need a much longer series of oxygen uptake experiments to find out just how flexible *Nautilus* is in this respect.

*Nautilus* oxygen uptake is sensitive to temperature change (Figure 2). The animal is known to move into shallower water at night, with vertical changes of as much as 200 m not uncommon on such occasions (WARD *et al.*, 1984). Given the steep temperature profiles found along reef slopes (see, for example, WARD & MARTIN, 1980) and the lack of time for temperature adaption during these excursions, *Nautilus* is likely to be altering its standard metabolic rate by a factor of two or three in daily cycles. We do not know what part these changes may play in the economic strategy of *Nautilus*, but it is conceivable that the animal is economizing by feeding during its nightly excursions into regions of higher temperature and then dropping down to

the cooler deeps to digest, as young salmon, for instance, are known to do in similar diurnal cycles (BRETT, 1983).

Given the information now available about oxygen consumption at rest and in activity, the  $Q_{10}$  and vertical migrations, temperature profiles off the reef face, and activity patterns, it is possible to construct an elementary energy budget for *Nautilus*. Crudely, with an oxygen uptake of around  $0.5 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$  at rest at  $17^\circ\text{C}$  and twice that at  $22^\circ\text{C}$ , and the animal spending half of every 24 h at each temperature (as indicated by records of vertical migrations in WARD *et al.*, 1984 and the temperature profiles given in WARD & MARTIN, 1980) the likely oxygen consumption over 24 h will be around  $1080 \text{ mL} \cdot \text{kg}^{-1}$ . To this must be added the cost of locomotion, being the difference between the active and resting oxygen consumptions, about  $0.75 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$  (the cost of transport will not vary

significantly with temperature). Accepting ZANN's (1984) figures for the proportion of time spent actively swimming ( $2.6 \text{ min} \cdot \text{h}^{-1}$  during the day and  $7 \text{ min} \cdot \text{h}^{-1}$  at night, with slightly higher figures at dawn and dusk) the added cost of locomotion is around  $110 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ . Taking one litre of oxygen to equal 4.6 kcal on a mainly protein diet broken down to ammonia, and a value for fish flesh of  $1.27 \text{ kcal} \cdot \text{g}^{-1}$  wet weight (an average from values given in WATT, 1968), and 95% absorption of food ingested at a cost of  $0.04 \text{ kcal} \cdot \text{g}^{-1}$  (as for *Octopus*, see O'DOR *et al.*, 1984), the daily requirement for a 500-g (flesh weight) *Nautilus* would be around 2 g of fish. A cropfull would keep the animal going for a month. This, it should be remembered, is based on the metabolic rates of fed animals. We know that the animal reduces its oxygen uptake by 50% after only three days of fasting. At this rate a square meal might last for a couple of months assuming zero growth but no loss of weight. *Nautilus* is evidently well suited to a scavenging life-style and an irregular food supply.

#### LITERATURE CITED

- BOUCAUD-CAMOU, E. & R. BOUCHER-RODONI. 1983. Feeding and digestion in cephalopods. In: A. S. M. Saleuddin & K. M. Wilbur (eds.), *The Mollusca*, Vol. 5:149-187. Academic Press: New York.
- BRETT, J. R. 1983. Life energetics of the sockeye salmon, *Oncorhynchus nerka*. In: W. P. Asprey & S. I. Lustick (eds.), *Behavioral energetics*. Ohio State Univ. Press.
- CARPENTER, J. H. 1966. New measurements of oxygen solubility in pure and natural waters. *Limnol. Oceanogr.* 11: 264-277.
- JOHANSEN, K., J. R. REDMOND & G. B. BOURNE. 1978. Respiratory exchange and transport of oxygen in *Nautilus pompilius*. *Jour. Exp. Zool.* 205:27-36.
- MANGOLD, K., A. PORTMANN & A. M. BIDDER. In press. *Traité de Zoologie*. Grassé (ed.).
- O'DOR, R. K., K. MANGOLD, R. BOUCHER-RODONI, M. J. WELLS & J. WELLS. 1984. Nutrient absorption, storage and remobilisation in *Octopus vulgaris*. *Mar. Behav. Physiol.* 11: 239-258.
- REDMOND, J. R., G. B. BOURNE & K. JOHANSEN. 1978. Oxygen uptake by *Nautilus pompilius*. *Jour. Exp. Zool.* 205:45-50.
- SAUNDERS, W. B. 1981. The species of living *Nautilus* and their distribution. *Veliger* 24:8-17.
- WARD, P. D. 1983. *Nautilus macromphalus*. In: P. R. Boyle (ed.), *Cephalopod life cycles*, Vol. 1:11-28.
- WARD, P. D., B. CARLSON, M. WEEKLY & B. BRUNBAUGH. 1984. Remote telemetry of daily vertical and horizontal movement of *Nautilus* in Palau. *Nature* 309:248-250.
- WARD, P. D. & A. W. MARTIN. 1980. Depth distribution of *Nautilus pompilius* in Fiji and *Nautilus macromphalus* in New Caledonia. *Veliger* 22:259-264.
- WATT, B. K. 1968. Composition of foods, raw and processed. Pp. 9-20. In: P. L. Altman & D. S. Dittmer (eds.), *Metabolism*. Fed. Amer. Soc. Exp. Biol.: Bethesda, Maryland.
- WELLS, M. J., R. K. O'DOR, K. MANGOLD & J. WELLS. 1983. Feeding and metabolic rate in *Octopus*. *Mar. Behav. Physiol.* 9:305-317.
- WELLS, M. J. & J. WELLS. 1985. Ventilation and oxygen uptake by *Nautilus*. *Jour. Exp. Biol.* 118:297-312.
- ZANN, L. P. 1984. The rhythmic activity of *Nautilus pompilius* with notes on its ecology and behavior in Fiji. *Veliger* 27: 19-28.